Dimethyl sulphide and *Phaeocystis*: A review

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Abstract

Dimethyl sulphide (DMS) is the dominant sulphur gas found in surface marine waters and there is compelling evidence that it is formed biologically in these environments. In all areas so far investigated the oceans are found to be highly supersaturated (typically by two orders of magnitude) with respect to atmospheric levels of DMS, which indicates a net flux of the gas out of the oceans. In this paper, we first briefly review the environmental importance of the gas and particularly the role of its sea-to-air flux on atmospheric chemistry and physics. Then we discuss what is known of its mode of formation and cycling in seawater, before looking more specifically at the role and significance of *Phaeocystis* as a producer of DMS.

1. Introduction

There are three main reasons why DMS is thought to be of importance in the environment. Firstly, studies of the global cycle of sulphur, published over the last three decades, have consistently indicated that in order to achieve balance, there has to be a substantial flux of volatile sulphur from the oceans into the atmosphere (estimates range from 1 to 6 × 10^{12} mol S yr^{-1}; see for example Eriksson, 1960; Junge, 1963; Robinson and Robbins, 1968; Kellog et al., 1972; Friend, 1973; Granat et al., 1976; Zehnder and Zinder, 1980; Ivanov and Freney, 1983). Earlier budgets attributed the flux to hydrogen sulphide from coastal areas but this is now considered to be unimportant. Since the work of Lovelock et al. (1972), it has become accepted that most of the flux is carried by DMS, with a small contribution from carbonyl sulphide which appears to be formed photochemically in seawater (Ferek and Andreae, 1984). The most recent budget is that of Brimblecombe et al. (1989) in which the global sea-to-air flux is given as 1.3 × 10^{12} mol S yr^{-1} (almost 90% of which is from the open oceans, with the rest from coastal regions). By comparison, 0.3 × 10^{12} mol S yr^{-1} is emitted from volcanoes to the atmosphere and about 3 × 10^{12} mol S yr^{-1} results from fossil fuel combustion.

There is, as yet, no direct way to determine the sea-to-air flux of DMS and emission rates are therefore estimated on the basis of empirical and theoretical considerations (Liss and Merlivat, 1986). The rate of transfer is calculated from the product of the concentration difference across the air–sea interface and a transfer (or piston) velocity. The transfer velocity is dependent inter alia on wind speed, water temperature and the presence of waves, bubbles and slicks.

Once in the atmosphere, DMS is subject to oxidation, principally by hydroxyl and nitrate radicals, to form acidic species including sulphur...
dioxide, sulphuric acid and methanesulphonic acid (Plane, 1989). This leads to the second major reason why DMS is environmentally important, i.e. via these oxidation products it is a major contributor to the acidity of atmospheric aerosols and rain, particularly in parts of the globe remote from man-made sources of sulphur dioxide (Charlson and Rodhe, 1982; Wagenbach et al., 1988; Savoie and Prospero, 1989). Even in Europe, less industrialised areas such as Eire, Norway and western Scotland can receive a significant amount of their atmospherically deposited sulphur in spring and summer from marine biogenic sources, including the north-eastern Atlantic and the North Sea (Fletcher, 1989; Tarra­son, 1991; Liss et al., 1993; Malin et al., 1993).

Five years ago a third role for DMS in the environment was suggested by Charlson et al. (1987). These authors proposed that in the marine atmosphere distant from land, the main source of the aerosol particles which act as cloud condensation nuclei (CCN) was sulphuric acid (partially neutralised by ammonia) derived from the oxidation of marine DMS. Since CCN are vital for droplet nucleation in clouds, which in turn controls the amount of solar radiation scattered by them as measured by their albedo, there is clearly an important role for DMS derived CCN in the radiation balance of the atmosphere. Charlson et al. (1987) went further still and suggested that the system had a climate regulating potential via a negative feedback mechanism between atmospheric (and hence oceanic surface water) temperature and the amount of DMS made by marine phytoplankton. That is, if the temperature of the atmosphere increases (by change in solar input or addition of radiatively active gases) then the concomitant warming of surface seawater might lead to an increase in DMS production and hence flux of the gas to the atmosphere. After oxidation, this would produce an increase in CCN and hence in cloud albedo; the result of which could be a cooling of the atmosphere, counteracting the original perturbation. Although there now seems to be general agreement on the importance of the oceans as a source of CCN in the remote atmosphere (Ayers and Gras, 1991; Ayers et al., 1991), there is currently large uncer­

2. The formation and cycling of DMS in seawater

Dimethyl sulphide is formed in seawater from the breakdown of its biochemical precursor, dimethylsulphoniopropionate (DMSP), according to the following reaction:

\[
\text{H}_3\text{C}—\text{S}^+—\text{CH}_2—\text{COO}^- \quad \text{DMSP}
\]

\[
\rightarrow (\text{CH}_3)_2\text{S} + \text{CH}_2\text{CHCOOH}
\]

The abundant sulphate ions in seawater (about 28 mmol in SO_4^{2-}) are the starting point for the formation of DMSP by cells. The synthesis occurs by assimilatory reduction of sulphate involving a complex, multi-step process (the details of which are not fully defined), in which important intermediates appear to be adenosine-5’-phosphos­ulphate, cysteine and methionine. The structure and zwitterionic nature of the DMSP molecule are consistent with its proposed role as an osmoregulatory solute in marine plankton (Iverson et al., 1989), and laboratory studies have shown how DMSP concentration correlates with salinity (Vairavamurthy et al., 1985; Dickson and Kirst, 1987a and b). Further, Kirst et al. (1991) have recently proposed that intracellular DMSP may act both as an osmolyte and as a cryoprotectant (antifreeze) in ice algae.

In culture studies DMSP and DMS are released from phytoplankton cells as they senesce (Turner et al., 1988), but in the natural environment it is likely that grazing by zooplankton is an important factor (Dacey and Wakeham, 1986). In
In this context, Leck et al. (1990) found significant correlations between DMS concentrations in the Baltic Sea and copepod and total zooplankton biomass. Additionally, the importance of microzooplankton grazing on phytoplankton in promoting release of DMSP and DMS is becoming increasingly acknowledged (Belviso et al., 1990).

Liberation of DMS from DMSP is known to be promoted by alkaline conditions, but at the pH of seawater (~8) the uncatalysed rate is extremely slow, having a half-life of about 8 years at 10°C (Dacey and Blough, 1987). However, Cantoni and Anderson (1956) and Ishida (1968) have shown that macro- and unicellular algae containing DMSP also have enzymes which catalyse cleavage of DMSP to DMS. Since DMSP is found free in seawater (Turner et al., 1988), as well as in phytoplankton cells, it seems likely that cleavage occurs both intra- and extracellularly; although the relative importance of these two modes of formation of DMS is not clear.

Compared with DMS, rather little attention has been paid to the other half of the cleaved DMSP molecule, i.e. acrylic acid. More than 30 years ago, Sieburth (1960) suggested that acrylic acid from DMSP could act as a broad spectrum antibiotic. Interestingly in the context of the present paper, Sieburth's proposal was made as a result of studies of blooms of *Phaeocystis* in Antarctic waters. More recently, Davidson and Marchant (1987) have noted that low bacterial numbers are associated with the mucilage of rapidly growing field or cultured colonies of *Phaeocystis*. However, they point out that any inhibitory effect of acrylic acid must depend on its concentration close to or on the cell walls, since it will be too diluted further from the cells to be effective.

A summary of many of our current ideas of the production and cycling of DMSP and DMS in the surface oceans is given in Fig. 1, which is taken from Malin et al. (1992). The figure shows that there are a number of sinks for DMS in addition to transfer across the sea surface, but it is currently not possible to properly quantify all these pathways. Brimblecombe and Shooter (1986) studied the photochemical oxidation of DMS to dimethylsulphoxide (DMSO) and concluded that the rate of loss via this route is approximately the same as that for passage across the air–sea inter-

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**Fig. 1.** The marine biogeochemical cycle of dimethyl sulphide (DMS); production, transformation and utilisation pathways which may ultimately influence the amount of DMS lost to the atmosphere (from Malin et al., 1992).
face. Kiene and Bates (1990) have recently shown that the rate of bacterial consumption of DMS can be more than ten times faster than the rate of outgassing to the atmosphere. Further, bacteria can oxidise DMS to DMSO (Zeyer et al., 1987), reduce DMSO to DMS under aerobic and anaerobic conditions (Zinder and Brock, 1978), and use DMS and DMSO as carbon and/or energy sources (Suylen, 1988). However, most of these studies have used cultures of non-marine bacteria, so it is difficult to assess their relevance to loss/transformation routes in seawater.

The complexity of the proposed cycle (Fig. 1) means that prediction of fluxes of DMS across the sea surface starting from biological production of its precursor is impossible given our present limited knowledge of the various parts of the cycle. Thus, for the foreseeable future we will need to rely on measurements of surface water concentrations of DMS and a knowledge of the transfer velocity of the gas in order to estimate sea-to-air fluxes (Liss et al., 1993). What is becoming clear, however, is that the loss of DMS to the atmosphere is a relatively small fraction of the larger cycle operating within the upper part of the oceans.

The level of DMSP per unit of phytoplankton biomass is variable and we are gradually unravelling the controlling factors, which include species composition, nutrients and temperature. Most significant is the type of phytoplankton; field and culture studies have shown that dinoflagellates and prymnesiophytes are the major DMSP producers, although there is considerable variation within classes (Holligan et al., 1987; Turner et al., 1988, 1989; Keller et al., 1989a; Malin et al., 1993). We return to this topic later in the paper.

Some data suggest that nutrient availability may also affect the level of intracellular DMSP, although the only evidence is for nitrate (Turner et al., 1988; Leck et al., 1990). Amongst the range of possible compatible solutes is glycine betaine, which is chemically very similar to DMSP but with nitrogen as the central atom, rather than sulphur (Blunden and Gordon, 1986). It has been suggested by Andreae (1986) that when nitrate levels are low, algae may have the ability to increase synthesis of DMSP and reduce production of glycine betaine, thus enabling a redirection of limited nitrogen resources to more fundamental requirements. Turner et al. (1988) advance two lines experimental evidence to support this idea. Firstly, they found that cultures of the coccolithophore *Emiliania huxleyi* produced less DMSP when grown with high nitrate concentrations than under low nitrate conditions. Secondly, for geographically adjacent samples from the North Sea having no clear differences in species composition, the level of DMSP in the cells was higher for samples where nitrate is below the analytical detection limit (<0.2 μmol) than for samples containing detectable amounts of NO₃⁻ (two groups significantly different at the 99.8% confidence limit). Although limited, these results do indicate the possibility of nutrient availability as one factor affecting the formation of DMSP.

We conclude this section with some comments on the spatial and temporal variability of DMS concentrations measured in marine waters. Andreae (1986, 1990) has summarised much of the field data and categorised it in terms of four types of ocean region, as shown in Table 1. Although approximately one and a half thousand data points went into constructing Table 1, there

<table>
<thead>
<tr>
<th>Ocean region</th>
<th>Average DMS (nmol⁻¹)</th>
<th>(s.d.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oligotrophic (e.g. Tropical North Atlantic and Pacific)</td>
<td>2.4</td>
<td>0.04</td>
</tr>
<tr>
<td>Transitional (e.g. Temperate N. Atlantic and Pacific)</td>
<td>2.1</td>
<td>0.17</td>
</tr>
<tr>
<td>Upwelling (incl. frontal, coastal and equatorial areas)</td>
<td>5.4 (4.9)</td>
<td>0.30</td>
</tr>
<tr>
<td>Coastal and shelf (incl. USA, North Sea and S. America)</td>
<td>2.7 (2.8)</td>
<td>0.12</td>
</tr>
</tbody>
</table>

From: Andreae, 1986, with revised estimates in Andreae (1990) shown in brackets.
are still very considerable gaps in the geographic coverage of the oceans (for example in the southern Atlantic and Pacific, and especially the Indian and Southern Oceans) and no attention has been paid to seasonal changes in concentration. In coastal areas the spatial variability is generally more marked than in the open oceans. Fig. 2 (from Liss et al., 1993) is an example from the southern North Sea in May of 1989 and shows that variations of up to two orders of magnitude can be observed, particularly at times of high biological activity.

There is rather little information available on seasonal cycles for DMS. In temperate coastal and shelf waters, such as the North Sea, a well marked cycle is apparent, as shown in Fig. 3 (from Liss et al., 1993). In the open oceans, the seasonal effect still appears to be present, although of decreased amplitude (Bates et al., 1987; Galloway et al., 1993). These attempts to construct the seasonal cycle in the open oceans are, of necessity, compilations of a limited number of data sets, which do not offer detailed geographical or seasonal coverage. It is, therefore, impossible at present to say how the size of the oceanic seasonal cycle varies with latitude.

Given that the production of DMSP is a biologically driven process, the existence of these variations in space and time is to be expected. However, even if the production process was well understood, it would still be necessary to have a quantitative knowledge of the various compo-
ments of the cycle shown in Fig. 1 before the water concentration of DMS, and hence the flux, could be predicted.

3. **Phaeocystis** and the formation of DMS

In the previous section we outlined several of the factors which are important for DMSP/DMS production and cycling in the marine environment, including the significance of phytoplankton speciation. Using various sources of information, we now attempt to review inter-species differences with respect to DMS and DMSP formation and assess the significance of **Phaeocystis** relative to other organisms in this regard. Further, if we are to model the system it is clearly necessary to understand not only what species are present in the water but also their capacities for formation of DMSP/DMS.

**Phaeocystis** has long been recognised as a particular "nuisance" species of phytoplankton (because, for example, it can clog fishermen's nets and cause foams on beaches), and there is also much anecdotal evidence to suggest it is a powerful source of DMS. Amongst several unflattering names for waters containing large numbers of the organism are "stinking waters", "bacey juice" and "weedy water". Although it has been the subject of scientific study for some time, it is only relatively recently that **Phaeocystis** and DMS have been studied simultaneously. There are not a great deal of data for DMS, let alone DMSP, along with measurements of **Phaeocystis** (Table 2). The records come from several very different and geographically widespread environments. Further, the DMS levels are generally considerably above the global average values shown in Table 1. Indeed, the results from Davis, Antarctica and the Weddell Sea represent the highest DMS values reported from anywhere in the world.

Further evidence for the importance of **Phaeocystis** as a producer of DMSP/DMS comes from the detailed assay of more than a hundred individual phytoplankton clones carried out by Keller et al. (1989a and b). Table 3 shows how DMSP per unit cell volume varied for three classes of the phytoplankton they assayed, together with some specific examples. It is apparent from the Table that prymnesiophytes, including **Phaeocystis**, are consistently strong producers. For the dinoflagellates, some are even more prolific producers than the prymnesiophytes but some form only small amounts. It is clear that diatoms are poor or non-producers.

Comparison of the laboratory culture findings with field results is difficult, not only because...
there is very limited data but more importantly because the occurrence in the field of samples containing only one species of phytoplankton is extremely rare, so that attribution of DMSP to specific organisms has inherent uncertainty. However, Table 4 is a compilation of our own field observations in U.K. coastal and shelf waters and the north-eastern Atlantic. Data have only been included when they are derived from samples where a large part of the total organic carbon (inferred from species counts) was from one, identifiable plankton species. Here the results are expressed as the ratio of DMS to chlorophyll a and total DMSP (i.e. dissolved in the water plus that contained in organisms) to chlorophyll a. Once again Phaeocystis is seen to be a consistently strong producer but it is clear that other species, particularly coccolithophores such as Emiliania huxleyi and Coccolithus pelagicus, also have a considerable ability to form DMSP/DMS.

As previously, diatoms appear to make much lower amounts of these compounds.

Additional evidence for the ability of Phaeocystis to form substantial amounts of DMSP/DMS comes from a study we carried out in the southern North Sea in May 1986. Sample analysis included DMS, DMSP and chlorophyll a, as well as phytoplankton identification and enumeration. The results are shown in Fig. 4 in which DMS + DMSP (total) is plotted against chlorophyll a, with the dominant species of phytoplankton indicated where it constituted more than 50% of the phytoplankton carbon. For diatom dominated samples, chlorophyll levels span the whole range found on the cruise, but DMS + DMSP concentrations were low and showed no clear increase with chlorophyll level. In contrast, samples dominated by Phaeocystis were found to contain much higher levels of DMS plus DMSP, with a clear increase in concentration with rise in chlorophyll (r = 0.85). Data for DMS from this cruise are included in Table 2.

It is clear that blooms of Phaeocystis can lead to very high levels of DMSP and DMS in the cells and surrounding water. A number of lines of argument can be advanced to try to explain why this is so. Several authors have noted that Phaeocystis tends to dominate over other phytoplankton species (e.g. Sieburth, 1979; Smayda, 1980; Lancelot et al., 1987). This may be because the organism has a competitive advantage over other phytoplankton species in that the mucus matrix surrounding the colonial cells can serve as a reservoir for carbon compounds (polysaccharides), vital nutrients such as phosphorus (Veldhuis and Admiraal, 1987) and trace metals like manganese (Davidson and Marchant, 1987; Lubbers et al., 1990).

Further, Marchant et al. (1991) suggest that the success of Phaeocystis in Antarctic waters may be related to the ability of colonies to produce extracellular UV-B protecting compounds in response to ambient UV-B levels. It is interesting to speculate that this ability might give Phaeocystis a competitive advantage over other types of phytoplankton, as UV-B levels further increase as a result of stratospheric ozone depletion.

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**Table 3**

<table>
<thead>
<tr>
<th>Species</th>
<th>Concentration (μmol DMSP/cm³)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phaeocystis</em> pouchedii</td>
<td>260</td>
</tr>
<tr>
<td><em>Phaeocystis</em> sp.</td>
<td>113</td>
</tr>
<tr>
<td><em>Emiliania huxleyi</em></td>
<td>166</td>
</tr>
<tr>
<td><em>Pleurochrysis carterae</em></td>
<td>170</td>
</tr>
<tr>
<td><em>Chrysochromulina pohylepis</em></td>
<td>192</td>
</tr>
<tr>
<td><em>Chrysochromulina polylepis</em></td>
<td>395</td>
</tr>
</tbody>
</table>

*(After: Keller et al., 1989a and b)*

* Provisional identification only; results for two different clones.
* σ(n – 1).
ND = not detectable.
The evidence for zooplankton grazing of Phaeocystis is confused; most studies showing that copepods ingest this species have used unialgal cultures and so do not prove that Phaeocystis is a preferred food source. Verity and Smayda (1989) found that Phaeocystis was not as good a food source for Acartia spp. as Skeletonema costatum, a chain-forming diatom, irrespective of whether free-living cells or colonies were used as the prey. The low grazing and egg production rates they observed when a unialgal diet of Phaeocystis was used (of the same order as for starved zooplankton) could have been due to Acartia spp. showing a preference not to ingest Phaeocystis due to its poor nutritional quality or unpalatability. It is interesting to note that copepods are chemosensory feeders and may avoid Phaeocystis due to production of DMS and acrylic acid or other physical or chemical properties of the colonial matrix. Since the above ideas are from laboratory studies, it should be stressed that their applicability in the field is not established and much further work needs to be done on this aspect.

All the above factors mean that within a bloom there will be production of considerable amounts of DMSP which, relative to more readily grazed phytoplankton, will tend to stay within the cells and surrounding mucilage. Indeed, it may be that even if the cells release some of their DMSP it is retained in the mucus. Also, we may speculate that, as suggested by Sieburth (1960), any cleavage of DMSP will lead to production of acrylic acid which may help to prevent bacterial settlement on and consequent degradation of the mucus. In the absence of grazing, major release of DMSP to the water will not occur until the cells die and lyse. This will lead to a rather rapid conversion of the large pool of intracellular DMSP to free DMSP and DMS in the water, and may be the explanation for some of the very high concentrations reported in association with Phaeocystis blooms (Table 2). In addition, Phaeo-

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**Table 4**

DMS and DMSPt (total) chlorophyll a ratios for different species of phytoplankton in European coastal and shelf waters

<table>
<thead>
<tr>
<th>Species</th>
<th>% Total carbon</th>
<th>S/Chl.a ratio *</th>
<th>n</th>
<th>Area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cyrodiplidium aureolum</td>
<td>&gt; 80</td>
<td>16 (18)</td>
<td>18</td>
<td>A</td>
</tr>
<tr>
<td>Ceratium lineatum</td>
<td>&gt; 77</td>
<td>115 (73)</td>
<td>6</td>
<td>B</td>
</tr>
<tr>
<td>Cyclotococcosphus leptoporus</td>
<td>&gt; 42</td>
<td>61 (38)</td>
<td>6</td>
<td>C</td>
</tr>
<tr>
<td>Coccolithophores (incl. E. huxleyi, C. pelagicus)</td>
<td>&gt; 50</td>
<td>170 (76)</td>
<td>16</td>
<td>D</td>
</tr>
<tr>
<td>P. pouchetii</td>
<td>&gt; 80</td>
<td>24 (17)</td>
<td>11</td>
<td>E</td>
</tr>
<tr>
<td>P. pouchetii</td>
<td>&gt; 50</td>
<td>172 (92)</td>
<td>4</td>
<td>F</td>
</tr>
<tr>
<td>P. pouchetii</td>
<td>a</td>
<td>26 (8)</td>
<td>4</td>
<td>G</td>
</tr>
<tr>
<td>P. pouchetii</td>
<td>o</td>
<td>35 (10)</td>
<td>6</td>
<td>H</td>
</tr>
<tr>
<td>P. pouchetii</td>
<td>a</td>
<td>83 (34)</td>
<td>16</td>
<td>I</td>
</tr>
<tr>
<td>Diatoms</td>
<td>b</td>
<td>4 (2)</td>
<td>9</td>
<td>J</td>
</tr>
</tbody>
</table>

*10^{-3} mol S m^{-3}/mg Chl.a m^{-3}, (n = 1).

Explanatory Notes for DMS and DMSPt/Chl.a Ratio:

*a*: Visual observations of colonies, Chl.a > 5 mg m^{-3}.

*b*: Visual observations of bloom, Chl.a > 3 mg m^{-3}.

A: July/Aug. 1985, English Channel.

B: July/Aug. 1985, Orkney Islands.

C: July/Aug., 1985, West of Scotland.


E: May, 1986, southern North Sea.


G and H: April, 1989, southern North Sea.

I: May, 1989, southern North Sea.

J: April, 1989, off East Anglia.
Fig. 4. DMS + DMSP (total) plotted against Chlorophyll a for samples from the southern North Sea in May 1986. Samples have been divided into four groups, in three of which one type of plankton constituted > 50% of the total biomass (+ Phaeocystis; ▲ diatoms; ◆ Chattonella sp.) and a fourth in which no single identifiable group was dominant (●).

Phaeocystis tends to bloom under calm conditions which implies that relatively small amounts will be lost to the atmosphere at that time (although subsequent high winds would lead to increased sea-to-air fluxes).

4. Discussion and conclusions

In this paper, we have attempted to describe the importance of marine biogenic DMS production with respect to three aspects of environmental chemistry, i.e. the global sulphur cycle, acidity of rain and aerosols and in the formation of cloud condensation nuclei with their implications for the radiation budget of the Earth.

Further, we have briefly reviewed current understanding of the formation and cycling of DMS in surface seawaters. A major conclusion is that the one-way flux of DMS to the atmosphere seems to be a relatively small bleed from the inter-linked bacteriologically and photochemically driven processes which transfer and transform DMSP/DMS within the upper ocean layers.

Although there are rather few studies to date which have looked specifically at the association between Phaeocystis and DMSP/DMS production, those which have been carried out imply a strong linkage, with this organism appearing to be able to produce and sustain high levels of these compounds. There is also some indirect evidence that blooms of Phaeocystis may be of particular interest for mechanistic studies of air-sea gas (including DMS) exchange. Firstly, Phaeocystis produces large quantities of mucus which may affect the viscosity of the water and hence the rate of gas transfer (Jenkinson, 1986). In a study of cultures (not including Phaeocystis), Frew et al. (1990) observed that phytoplankton exudates, such as heteropolysaccharides, could affect near-surface turbulence and lead to decreased gas exchange rates. Secondly, Stramska et al. (1990) found in laboratory studies that seawater supersaturated with the major atmospheric gases produced increased numbers of aerosols droplets. From this one might speculate that Phaeocystis, which can produce oxygen supersaturations of up to 160% (for example in the southern North Sea, D. Purdie, pers. commun., 1986), may also indirectly enhance gas transfer. The extent to which these opposite effects operate in the field is unknown, but worthy of further study.

Phaeocystis is an organism with a widespread occurrence. The map of its distribution published by Kashkin (1963) shows it occurs over large areas of Antarctic waters and the north-eastern Atlantic, inter alia. Smith et al. (1991) have recently reported on the significant role the organism plays in the carbon cycle across much of the Greenland Sea. Further, in many coastal and shelf areas the importance of Phaeocystis has been well recognised for many years. Indeed, such inshore regions have received considerably
more attention than the open oceans. Examples of such studies include several for the southern North Sea (coastal waters off Belgium — Lancelot and Mathot, 1987; Holland — Gieskes and Kraay, 1977; Veldhuis et al., 1986a, b; Germany — Eberlein et al., 1985; Bätje and Michaelis, 1986; Weisse et al., 1986), the Irish Sea (Jones and Haq, 1963; Claustre et al., 1990), Narragansett Bay, R.I., U.S.A. (Verity and Smayda, 1989) and the Barents Sea (Wassmann et al., 1990). To reinforce the importance of such studies it is noteworthy that it has been calculated that in parts of the southern North Sea (e.g. in Belgium coastal waters) more than 65% of the annual primary production is due to Phaeocystis (Lancelot, 1984).

There has been discussion in the literature as to whether the cosmopolitan Phaeocystis is, in fact, a single species (e.g. Sournia, 1988). The taxonomic identity of Phaeocystis has been reviewed by Baumann et al. (1994) by comparing the morphological and physiological characteristics of Phaeocystis cells and colonies of different geographical origin. This analysis gave evidence for four species — P. globlosa, P. scrobiculata, P. pouchetii and one undefined Antarctic species — distinguishing themselves by colony and free-living cell morphology and temperature tolerance. Accordingly, different isolates have also been shown to have different arrays of pigments (e.g. Claustre et al., 1990). UV-B related studies show differences between Phaeocystis isolates from Antarctica and the east Australian current (Marchant et al., 1991). To date little is known regarding variation in cellular DMSP concentrations of different Phaeocystis isolates, although Keller et al. (1989a) found a factor of two difference between two clonal cultures. Many questions remain to be answered, e.g. could differences in the ability to produce DMSP and/or the reasons for its production (osmoregulation and/or cryoprotection) account for the extremely high DMS/DMSP concentrations reported for Antarctica (Table 2)?

We conclude that Phaeocystis deserves further study in view of its widespread abundance and ability to form DMSP/DMS. Such studies should incorporate complementary measurements of the biologically driven carbon and sulphur systems. Only then can a proper assessment be made of the quantitative role played by Phaeocystis in the global cycle of sulphur and its ramifications for atmospheric chemistry and physics.

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